

Hill, D. L., Pillay, N., Schradin, C. and Loison, A. (2015) Alternative reproductive tactics in female striped mice: heavier females are more likely to breed solitarily than communally. *Journal of Animal Ecology*, 84(6), pp. 1497-1508.

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Hill, D. L., Pillay, N., Schradin, C. and Loison, A. (2015) Alternative reproductive tactics in female striped mice: heavier females are more likely to breed solitarily than communally. *Journal of Animal Ecology*, 84(6), pp. 1497-1508, which has been published in final form at <http://dx.doi.org/10.1111/1365-2656.12431>

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Deposited on: 20 February 2020

Alternative reproductive tactics in female striped mice: heavier females are more likely to breed solitary than communally

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Key-words alternative phenotypes; breeding synchrony; cooperative breeding; phenotypic
plasticity; plural breeding; polyphenism; reproductive competition; single breeder; social
flexibility; sociality

Summary

1. Alternative reproductive tactics (ARTs) are discrete reproductive phenotypes governed by decision-rules called strategies. ARTs are fixed for life in species with alternative strategies, while tactic expression is plastic in species with a single strategy. ARTs have been investigated in males of many species, but few studies have tested whether the same theoretical framework applies in females.
2. Female striped mice (*Rhabdomys pumilio*) employ three ARTs: communal breeders give birth in a nest shared with female kin and a breeding male, and show alloparental care; returners give birth away from the shared nest and later return to it; and solitary breeders give birth away from the shared nest and do not return to the group.
3. Here, studying free-living female striped mice over six breeding seasons, we tested whether ARTs arise from alternative strategies or a single strategy.
4. We also asked to what extent stochastic extrinsic factors explain whether individuals become solitary rather than group-living.
5. Females switched tactics, consistent with a single strategy, so we tested whether this represented a mixed or conditional single strategy. Only the latter predicts differences between ARTs in traits indicating competitive ability, such as body mass or age, before individuals adopt a tactic. We weighed females at conception when they were still group-living to eliminate potential confounding effects of gestation and subsequent social tactic (solitary- versus group-living) on body mass.
6. Females that went on to use a solitary ART were heavier than those that became communal breeders and returners, in support of a conditional strategy.
7. Importantly, solitary breeders also arose through extrinsic factors (mortality of all adult female group members). They weighed less than females that became solitary

while relatives were alive, but did not differ in body mass from communal breeders and returners.

8. We conclude that ART theory applies to both sexes, with female striped mice following a conditional single strategy. Future studies should consider the possibility that phenotypes that superficially resemble evolved tactics might also arise through non-adaptive extrinsic causes.

Introduction

A primary aim of life history theory is to understand the factors that influence reproductive decisions. *Alternative reproductive tactics* (ARTs) are discrete reproductive phenotypes shown by different members of the same sex and population and governed by genetically-based decision-rules called *strategies* (Dominey 1984; Gross 1996). Individuals following alternative tactics differ in behavioural, morphological, physiological and/or life history characteristics. Individuals are said to use *alternative strategies* when different tactics are controlled by different genotypes (Gross 1996), and *single strategies* when a single genotype controls different tactics (Schradin & Lindholm 2011). At the phenotypic level, ARTs are fixed for life in individuals following alternative strategies, while their expression is plastic under a single strategy (Fig. 1).

The term single strategy was introduced to describe systems where one decision-rule can produce multiple phenotypes (Fig. 1) regardless of whether fitness differences between ARTs occur (which can depend on environmental conditions) (Schradin & Lindholm 2011). Such decision-rules are traditionally divided into mixed and conditional strategies (Fig. 1). A *mixed strategy* occurs when tactics are expressed on a probabilistic basis rather than in response to environmental or individual-level cues (Dominey 1984). Individuals employing a *conditional strategy*, by contrast, are predicted to select the tactic that generates the highest fitness returns for their prevailing state or status (status-dependent selection model; Gross 1996). Individuals frequently differ in continuous traits associated with competitive ability, such as body mass or age. When the tactic that yields the highest fitness (often called the bourgeois tactic) is also the most costly to employ, only the most competitive individuals will be able to use it (Gross 1996). Less competitive individuals will thus employ a different tactic that yields a lower

fitness but is the highest fitness they can achieve at the time, known as ‘making the best of a bad job’ (Dawkins 1980). Under a conditional strategy, individuals should express a particular tactic when they pass a threshold (*switchpoint*) for the indicator trait after which the fitness benefits for that tactic are greater than what they could achieve using an alternative tactic (Hazel, Smock & Johnson 1990). They may switch from one tactic to another, for example, when they reach a certain age or size. The environmental-threshold model predicts that selection acts upon heritable genetic variation for the position of the switchpoint, so different individuals might express a given tactic at different values of the indicator trait (reviewed in Tomkins & Hazel 2007).

ARTs have been studied extensively in males, but are less well understood in females. Female ARTs include monandry versus polyandry in horseshoe crabs (*Limulus polyphemus*) (Johnson & Brockmann 2012) and brood parasitism versus maternal care in goldeneye ducks (*Bucephala clangula*) (Åhlund & Andersson 2001). ARTs often evolve where there is pronounced intra-sexual variance in fitness and intense reproductive competition (Shuster 2008). These conditions apply more frequently in males than in females, which probably explains the greater prevalence of male ARTs (Neff & Svensson 2013). However, intense reproductive competition also exists between females (Clutton-Brock 2009), and the number of studies of female ARTs has increased in recent years, suggesting that they were previously overlooked. This balance needs to be redressed to achieve a comprehensive, sex-independent understanding of ARTs.

Few studies to date have investigated the factors leading to the evolution of female ARTs and whether the theory governing male ARTs applies to females. The striped mouse (*Rhabdomys pumilio*) is a good species in which to address these issues because ARTs occur in both sexes,

with males and females either breeding solitarily or in groups. Breeding groups typically consist of 2-4 closely related females, one male and their communal offspring (Schradin & Pillay 2004). Communally-breeding females often give birth synchronously and provide allo-parental care, including allo-nursing (Schradin, Kinahan & Pillay 2009a; Schubert, Pillay & Schradin 2009). Nevertheless, reproductive competition occurs between females through aggression and infanticide (Schradin, König & Pillay 2010), and females can become solitary during the breeding season if unoccupied territories are available (Schradin, König & Pillay 2010; Schoepf & Schradin 2012a). While the ratio of communal to solitary females increases with increasing population density, both solitary and group-living females co-occur under most conditions (Schradin, König & Pillay 2010; Schoepf & Schradin 2012a). In addition to these solitary and communal breeding female tactics, we report here for the first time the tactic of *returner*, where females give birth away from the natal group but later return to it.

Group-living females might become solitary as part of a strategy to optimize fitness or alternatively because of extrinsic factors that constrain them to rear young alone (Schradin 2013). Groups are limited to close kin in many social species, and these groups can be reduced to a single solitary individual by natural mortality. This can occur in populations with small group sizes and high predation, such as Callitrichid primates (Anzenberger & Falk 2012). In the absence of information on group history, such individuals might be mistakenly assumed to be following a solitary ART. However, in such cases, solitary-living is not the result of a strategy (an evolved set of rules), and cannot be explained by ultimate or proximate causes at the individual level (Schradin 2013). Therefore, when observing solitary versus group-living members of the same population, it is important to consider the possibility that solitary-living is not a tactic, but the result of stochastic processes. To our knowledge, this has not been considered in any previous study on ARTs.

108

109 Here, we explored the following questions in female striped mice: (i) Do ARTs arise from
110 alternative strategies or a single strategy? We addressed this by testing whether females
111 switched ARTs, which would indicate a single strategy. Females did switch ARTs, and so we
112 asked (ii) whether this represented a mixed or a conditional strategy. Under a conditional (but
113 not mixed) strategy, females that go on to adopt different tactics are predicted to differ from
114 each other in individual-level traits that reflect competitive ability. We examined body mass
115 because it is associated with competitive ability (Schradin 2004) and aggression (Schoepf &
116 Schradin 2012b) in this species, and because male striped mice following alternative tactics
117 differ in body mass (Schradin *et al.* 2009b). To decouple the predicted effect of body mass on
118 tactic choice from the confounding effects of following different tactics on body mass, all
119 females were weighed when they were still group-living. We also considered age, which is
120 related to aggression in striped mice (Schoepf & Schradin 2012b) and to rank in many co-
121 operatively breeding species (Creel *et al.* 1992). We predicted that females that go on to
122 breed solitarily would be heavier and/or older than communal breeders. Next, we examined
123 breeding synchrony to test whether females leave the group to avoid reproductive
124 competition. In communally-breeding groups, earlier-born litters suffer an increased risk of
125 infanticide from gestating females, while later-born litters may be unable to compete with
126 older ones (Hodge, Bell & Cant 2011). We predicted that group-living females would be
127 more closely synchronized with nestmates than with females from other groups, and that
128 females that were less synchronized with nestmates would be more likely to adopt a solitary
129 or returner tactic than to breed communally. Finally, we asked (iii) whether solitary breeding
130 is always the outcome of a strategy or if it can also arise from entirely extrinsic factors
131 (mortality of all other adult female group members). If the latter scenario occurs, we would
132 expect females constrained to breed solitarily by the death of relatives to be of a lower body

mass or age than solitary breeders with living relatives (which are predicted under ii to be subject to status-dependent selection for increased body mass or age), but to be similar in body mass and age to communal breeders.

Materials and Methods

STUDY SITE

Fieldwork took place every month during the years 2005 to 2010 in Goegap Nature Reserve, Northern Cape Province, South Africa (S 29 41.56, E 18 1.60). The study area is Succulent Karoo and consists of an open habitat of shrubs, grass and sandy areas. It receives 180mm precipitation *per annum*, which mostly falls between April and July. Minimum ambient temperature (T_a) was recorded in the shade 5cm above the ground at the study site each day.

LIVE-TRAPPING AND BEHAVIOURAL OBSERVATIONS

Striped mice are diurnal and nest in shrubs at night. They rarely experience more than one breeding season, so each year of study represents a new generation. Individuals were captured using Sherman-type live-traps (26×9×9cm) baited with bran flakes, sunflower oil and salt. Traps were set in the shade close to nest sites at dawn and in the afternoon, and checked twice in the morning and once at dusk, 30-45 minutes after being set. We placed 3-20 traps (depending on group size) at several nest sites for 3-4 consecutive days throughout the year to allow each group to be monitored on rotation every two weeks. Newly-trapped individuals were provided with numbered aluminium ear-tags (National Band and Tag, Newport, KY) for identification, and marked with hair dye (Inecto, Pinetown, South Africa) so that they could be recognized during behavioural observations at nest sites (see below).

Adults were fitted with MD-2C radio-collars (Holohil, Canada), which weighed 2.5g, representing $5.4 \pm 0.07\%$ of the body mass of non-gestating females ($n=181$ records from 110 females). Females were weighed to the nearest gram using an electronic balance, and nipples were classified as pink and elongated (suggestive of lactation), otherwise visible or not visible.

Juveniles (body mass $<30\text{g}$) were assumed to originate from the nest where they were first trapped and observed affiliating with group members during behavioural observations. This method was validated using microsatellite markers (Schradin & Lindholm 2011). Behavioural observations took place at nest sites at dusk when striped mice were returning from the day's foraging. We observed marked individuals through binoculars for 30 minutes from a distance of $\sim 10\text{m}$, and recorded affiliative and aggressive interactions as described in Schradin and Pillay (2003). Observations were carried out on all focal groups on rotation throughout the year, except that a given group was not subject to both trapping and behavioural observations on the same day. As genetic data show that female group members are close kin (C. Schradin and A. K. Lindholm, unpublished data), we refer to females that nested together (or did so before becoming solitary) as 'relatives'.

RADIO-TRACKING

Striped mice were radio-tracked 4-5 nights a week throughout the breeding season using an AR8000 wide-range receiver (AOR, Tokyo, Japan) and an H-antenna. We approached potential nest sites from different angles until we located the source of the radio-signal. We assumed that individuals were sharing a nest when their signals derived from the same position. This allowed us to determine the location of nests, the identity of all adults in a nest and the date that individuals changed nest sites. Individuals leave the nest by day to forage, so

we also radio-tracked them once during the day to confirm that radio-collars had not been discarded in the nest. Locations of individuals and nests were recorded using an eTrex Venture GPS (GARMIN, Olathe, KS), which was accurate to ~5m at our study site. We maintained continuity of group identities between breeding seasons by radio-tracking one female from each group during the non-breeding seasons, when group membership is stable (Schoepf & Schradin 2012; Schradin, König & Pillay 2010). Radio-collars were removed from all other group members at the end of each breeding season.

DETERMINATION OF ALTERNATIVE REPRODUCTIVE TACTIC

Striped mice give birth in the austral spring (August to December). For each female fitted with a radio-collar, we plotted body mass records from July to January of each year against the date. We examined individual plots for the rise and sudden fall in body mass indicative of gestation and parturition. We assumed that parturition occurred on the median day within each trapping interval (the period between a female's last trapping antepartum and her first trapping postpartum) unless we could refine our estimate from observational data. We checked whether the estimated parturition date was consistent with a change in lactation status. Females were classified as *nesting communally* (sharing a nest with ≥ 1 adult female) or *not nesting communally* on the night before parturition. The latter category was divided into three subcategories: a) *returners*: those that nested with their original group ≥ 1 night after parturition; b) *solitary breeders with relatives*: those that did not nest with the group after parturition although former (female) nestmates were still alive; and c) *solitary breeders without relatives*: females whose female nestmates were no longer living. We refer to the four categories (communal breeder, returner, solitary breeder with relatives, solitary breeder without relatives) as *reproductive phenotypes*, and the first three of these categories (i.e. those that are not determined by mortality of all female relatives; see Introduction) as *ARTs*. We

ensured that solitary females were not nesting with unmonitored females by only considering groups where all adult females were wearing radio-collars when relatives gave birth, and by observing the identity of individuals returning to nests during behavioural observations.

ESTIMATION OF AGE AT PARTURITION AND BODY MASS AT CONCEPTION

Age at parturition (AP) was calculated as the difference between a female's estimated parturition date and her date of birth; date of birth was estimated from the population-specific growth curve in Schradin, Schneider & Yuen (2009c). We estimated the date that females conceived by subtracting 23 days (the minimum period between litters in captive striped mice (Brooks 1982)) from the estimated parturition date. To estimate *body mass of females at conception* (BMC) we used the closest morning body mass record available up to 10 days before or three days after the estimated conception date. We only used morning data because females weighed less in the morning than at dusk (morning: $39.4 \pm 2.37\text{g}$, $n=12,515$ observations from 1917 females; dusk: $42.6 \pm 2.37\text{g}$, $n=6398$ observations from 1602 females; $\beta=3.17 \pm 0.13$, $t=23.84$, $P<0.001$, controlling for individual identity and year). BMC records were considered 'missing' if no morning values were available or if females were known to be gestating. Missing values for BMC and AP were filled in using multiple imputation (Appendix S1).

STATISTICAL ANALYSIS

We retained for statistical analysis all parturitions occurring between 1st August and 31st December in 2005 to 2010 where parturition date and reproductive phenotype could be determined ($n=243$ parturitions from 132 females from 33 groups; Table 1). Four females gave birth in two consecutive breeding seasons (two in 2005-06 and two in 2007-08); the remaining 128 individuals bred in a single season. Variation in monitoring effort is likely to

233 be a common feature of longitudinal field studies like ours, but is rarely reported. We present
234 annual survey effort in Table 1. *Parturition trapping interval* (PTI) and *radio-tracking effort*
235 were not associated with reproductive phenotype (Generalized and General Linear Mixed
236 effects Models, respectively, controlling for individual identity, group identity and year: PTI
237 $P \geq 0.059$; radio-tracking effort $P \geq 0.128$, adjusted for multiple comparisons). Mean annual
238 breeding synchrony was not correlated with PTI ($r_s = 0.49$, $P = 0.356$, $n = 6$).

239

Table 1. The numbers of groups and ‘focal’ females (i.e. females that gave birth while they and all female relatives were fitted with radio-collars), the number of parturitions for which radio-tracking data were available, adult population density at the start of the breeding season (Sept), the mean trapping interval within which females gave birth, and mean radio-tracking effort (the number of nights a female was tracked as a percentage of the number of nights she wore a radio-collar). Each year represents a new generation. Means are given (± 1 SE)

Year	No. focal groups	No. focal females	No. parturitions	Population density (adults/ha)	PTI (days)	Radio-tracking effort (%)
2005	8	14	17	19.0	12.1 \pm 2.44	32.9 \pm 2.05
2006	7	19	31	30.5	10.2 \pm 1.13	52.1 \pm 1.00
2007	12	29	59	6.5	7.2 \pm 0.96	67.1 \pm 0.70
2008	15	33	68	7.7	7.6 \pm 0.75	59.8 \pm 0.52
2009	9	23	43	10.4	6.5 \pm 0.73	50.9 \pm 0.65
2010	9	18	25	4.7	5.2 \pm 0.93	65.6 \pm 0.74

PTI is parturition trapping interval

(i) *Do ARTs arise from alternative strategies or a single strategy?* We determined whether female striped mice switch tactic (consistent with a single strategy), and estimated the probabilities of females moving from one tactic to another ('transition probabilities') in continuous time using a general multi-state Markov model. We considered all females with living relatives and >1 parturition, and assumed that individuals could move from any of the three states (communal, returner, solitary) to any other state in either direction or retain a single state. Transition probabilities for each state were modelled with 95% confidence intervals, accounting for individual identity and parturition date. We used the msm package (Jackson 2014) in R version 3.1.1. (R Development Core Team 2014).

(ii) *Do ARTs represent a mixed or a conditional strategy?* We tested for differences in individual-level traits between females that subsequently use alternative tactics, as expected under a conditional strategy. We used a multinomial Generalized Linear Mixed effects model because this allowed us to fit female ART as a nominal response variable with three levels (communal breeder, solitary breeder and returner) and BMC and AP as fixed effects. We focused on females whose relatives were alive when they bred because the aim was to understand tactic choice. We only considered females that were group-living when body mass was recorded (conception) to determine whether differences in body mass induce females to adopt different tactics, which can otherwise be confounded by the effects of employing a given ART on body mass. We controlled for T_a and the interaction between BMC and T_a because environmental conditions might affect females differently depending on their size or body reserves. We fitted random intercepts for individual identity, natal group identity and year to control for repeated measures. Considering natal group identity also allowed us to control for potential effects of territory quality and genetic relatedness between members of the same group, while 'year' allowed us to account for potential variation in

population density, predation, food availability and other unknown variables that might influence tactic choice between breeding seasons. The model was executed using the package MCMCglmm (Hadfield 2010; Hadfield 2012) in R; specifications and diagnostics are given in Appendix S2.

To evaluate breeding synchrony, we calculated the absolute number of days between all possible pairs of parturitions by different individuals up to a maximum of 23 days apart (the estimate of gestation length used in our study). Where a given parturition by female A occurred ± 23 days from two parturitions by female B (i.e. where B gave birth ≤ 23 days before A and again ≤ 23 days after A), only the record yielding the smaller date difference between the pair was retained in the dataset. We noted whether each pair of females shared a nest when they conceived ('nestmates'), originated in the same group but no longer shared a nest when they conceived ('related non-nestmates') or originated in different groups ('non-relatives'). We focused on females that were group-living when they conceived to test whether breeding asynchrony is associated with females leaving the group; records comparing related non-nestmates were discarded. For all records from nestmates, we determined the tactics used for each pair of parturitions. This produced a categorical variable ('pair category') with three levels for females that shared a nest when they conceived (communal vs communal, communal vs returner, communal vs solitary), and a fourth level for unrelated pairs where at least one female bred communally. Breeding synchrony data were analysed in a single Generalized Linear Mixed effects Model (GLMM) with Poisson errors using the lme4 package (Bates *et al.* 2014). The absolute number of days between two parturitions was the response variable, year and natal group identity were random factors and pair category was a fixed factor with four levels. We carried out a Dunnett multiple comparison test based on this model to compare synchrony within communal breeders (i.e.

pairs where both individuals were communally-breeding nestmates) with synchrony between communal breeders and the other three levels (returners, solitary breeders, non-relatives).

To investigate changes in the distribution of reproductive phenotypes over the breeding season we fitted a Linear Mixed effects Model (LMM) to data from all four reproductive phenotypes (including those that were already solitary at conception). BMC, AP, T_a and reproductive phenotype were fitted as fixed effects to ordinal parturition date (i.e. where 1st January of any year is day 1), controlling for female identity, group identity and year (random intercepts only). This allowed us to compare parturition dates among the different phenotypes.

(iii) Is solitary breeding always the outcome of a strategy or can it also arise from entirely extrinsic factors? Solitary-breeding phenotypes produced by extrinsic factors (mortality of all other adult female group members) occurred in the population, and so we tested whether they differed in individual-level traits from females using ARTs. BMC and AP were normally-distributed response variables in separate LMMs, and we fitted reproductive phenotype as a fixed factor with four levels. We controlled for fixed effects of T_a and random intercepts of female identity, group identity and year.

For all tests, significant effects are denoted by $P < 0.05$ or a credible interval (CrI hereafter) or confidence interval (CoI) that does not include zero. Continuous fixed effects were mean-centred to assist model convergence. LMMs were fitted by Restricted Maximum Likelihood using lme4 (Bates et al. 2014) and lmerTest (Kuznetsova, Brockhoff & Christensen 2014). Tukey or Dunnett contrasts allowed us to determine which levels of factors differed from each other, and P -values were adjusted using a single-step method (multcomp package:

Hothorn, Bretz & Westfal 2014). Statistical tests are two-tailed and means are least squares means \pm 1 SE.

Results

Did female striped mice switch ARTs, consistent with a single strategy?

Female striped mice with living relatives bred communally (40.7% of parturitions), as returners (42.7%) or solitarily (17.3%). Multiple breeding attempts within a single season were recorded for 55.0% of females with relatives ($n=120$ females with relatives: 1.8 ± 0.08 (range 1-4) litters), of which 57.6% switched ARTs at least once (Table 2). For females that bred more than once and did not switch tactic while relatives were living, the majority (46.4%) bred communally, 28.6% bred as returners and 25.0% bred solitarily (Table 2).

Table 2. The numbers of female striped mice that showed a single reproductive phenotype (RP: communal breeder, returner, solitary breeder with living relatives, solitary breeder without living relatives) and those that changed from one RP to another in a single breeding season. All females shown ($n=75$) produced at least two litters in a breeding season

RP	No. females
<i>Did not switch ARTs, female relatives alive</i>	28
Communal	13
Returner	8
Solitary	7
<i>Switched ARTs, female relatives alive</i>	38
communal → returner ^a	16
returner → solitary ^b	8
returner → communal ^a	6
communal → solitary	1
communal → returner → communal	3
returner → communal → returner	3
communal → returner → solitary	1
<i>RP caused by extrinsic factor: death of female relatives</i>	11
returner → solitary ^b	3
communal → solitary	1
solitary	7

^aOne female produced multiple litters in two consecutive seasons and is presented for the two seasons separately.

^bOne female belongs to both these categories because she bred as a returner then twice solitarily (once before and once after her relatives died).

Females that had living relatives and bred more than once were no more likely to switch tactic than to use the same tactic throughout the breeding season (probability of switching tactic: 0.58, 95% CoI=0.45 to 0.70, $P=0.268$, $n=66$; exact binomial test). A female's subsequent tactic depended on her previous tactic (likelihood ratio $\chi^2_4 = 44.60$, $P<0.001$; Fig. S1, Supporting information). Communal breeders were more likely to continue breeding communally ($\beta=0.013$, 95% CoI=0.0190 to 0.0087) or become returners ($\beta=0.012$, CoI=0.0078 to 0.0178) than to breed solitarily ($\beta=0.001$, CoI=0.0003 to 0.0041) on their next breeding attempt. Returners were no more likely to continue breeding as returners ($\beta=0.014$, CoI=0.0091 to 0.0209) than to switch to communal ($\beta=0.008$, CoI=0.0047 to 0.0140) or solitary ($\beta=0.006$, CoI=0.0029 to 0.0108) breeding. Among those that switched tactic, communal breeders were 11.5 times more likely to become returners (92 (CoI=82 to 103) %) than to become solitary breeders (8 (CoI=2 to 30) %).

Did individual-level traits influence ARTs, as expected under a conditional strategy?

BMC was associated with ARTs in female striped mice with living relatives (Fig. 2; Table 3), while AP, T_a and the interaction between BMC and T_a were not (Table 3). Solitary breeders with relatives were heavier at conception than females that bred communally and returners, but there was no difference in BMC between communal breeders and returners (Fig. 2). Among females that had living relatives and went on to breed solitarily, body mass did not differ between females that were group-living at conception (51.3 ± 1.87 , $n=18$ observations from 18 females that became solitary after conception), and those that were already solitary when they conceived (47.8 ± 1.90 , $n=19$ observations from 16 females; $\beta=3.52 \pm 2.04$, $t=1.72$, $P=0.099$, controlling for AP and T_a).

Table 3. Multinomial Mixed effects Model to test for the effects of body mass at conception (BMC), age at parturition (AP), minimum ambient temperature (T_a) and the interaction between T_a and BMC on ARTs in female striped mice with living relatives ($n=195$ records from 112 individuals that were group-living when they conceived). We fitted unique variance and co-variance structures for each ART ('communal breeder', 'solitary breeder', 'returner') interacted with each random term (individual identity, group identity and year; not shown). Parameter estimates (β) are modes from the posterior distribution with 95% credible intervals. Non-significant fixed effects were eliminated sequentially to reach the final model. Significant effects are in bold.

Fixed effects	β	p MCMC
communal breeder intercept	2.524 (0.603 to 4.586)	0.007
returner intercept	2.738 (1.147 to 4.535)	0.001
BMC ^a (communal)	-0.157 (-0.274 to -0.047)	0.003
BMC ^a (returner)	-0.121 (-0.230 to -0.016)	0.021
T_a^a (communal)	0.066 (-0.174 to 0.314)	0.605
T_a^a (returner)	0.132 (-0.099 to 0.369)	0.246
AP ^a (communal)	0.005 (-0.004 to 0.015)	0.290
AP ^a (returner)	0.005 (-0.004 to 0.014)	0.296
$T_a \times \text{BMC}^a$ (communal)	-0.024 (-0.052 to 0.003)	0.078
$T_a \times \text{BMC}^a$ (returner)	-0.023 (-0.049 to 0.003)	0.080

^a 'solitary breeder' is the baseline level of the response (reference group)

The returner tactic was more likely to occur because returners moved to a new nest ($n=69$ parturitions from 53 individuals) than because they stayed behind when their nestmates moved away ($n=18$ parturitions from 18 individuals; probability of returner tactic arising through movement of focal female versus relatives: 0.75, 95% CoI=0.63 to 0.84, $P<0.001$, exact binomial test). There was no difference between returners that moved and those that stayed behind in AP ($\beta=-0.005\pm0.003$, $Z=1.60$, $P=0.110$), BMC ($\beta=-0.02\pm0.04$, $Z=0.54$, $P=0.589$) or the number of females they shared a nest with before parturition ($\beta=0.25\pm0.17$, $Z=1.48$, $P=0.138$; GLMM with binomial errors controlling for individual and group identities and year). Groups were more likely to reunite because the returner moved back ($n=58$ parturitions from 46 individuals) than because the returners' relatives moved to join her at her new nest ($n=29$ parturitions by 27 individuals; probability of re-joining group owing to movement of returner versus relatives: 0.67 (0.56 to 0.76), $P=0.002$).

Returners gave birth 1.7 ± 0.35 (range 0-28) days after becoming temporarily solitary ($n=84$ parturitions by 63 females), and re-joined the group after 6.4 ± 0.61 (range 1-35) days alone. On average, they re-joined the group after their communally-breeding nestmates had given birth (mean difference= 7.7 ± 1.95 days; $t_{89}=3.82$, $P<0.001$, paired t-test). The interval between leaving the group and parturition was not influenced by BMC ($\beta=0.00002\pm0.01$, $Z=0.001$, $P=0.999$, GLMM with poisson errors controlling for individual and group identities and year) or AP ($\beta=-0.0006\pm0.001$, $Z=0.53$, $P=0.600$). Those that moved to a new nest stayed away for longer than those that stayed behind when their relatives moved away (changed nest: 6.8 ± 0.72 nights; stayed: 4.0 ± 0.65 nights; $\beta=0.40\pm0.18$, $Z=2.27$, $P=0.023$; GLMM with poisson errors). The number of nights that returners spent away was not related to BMC ($\beta=0.01\pm0.01$, $Z=1.41$, $P=0.158$) or AP ($\beta=-0.0002\pm0.001$, $Z=0.22$, $P=0.823$).

Females with living relatives were more likely to become solitary by moving to a new nest ($n=18$ individuals) than by remaining at the nest when their nestmates moved away ($n=7$; probability of becoming solitary by moving away: 0.72, 95% CoI=0.51 to 0.88, $P=0.043$). All seven females in the latter category had only one female relative, while those that moved to a new nest came from larger groups (1.9 ± 0.31 female nestmates, range 1-5; $Z=2.05$, $P=0.040$, asymptotic Wilcoxon Rank Sum Test). There was no difference between solitary females that moved to a new nest and those whose nestmates moved in age ($\beta=0.001\pm0.003$, $Z=0.25$, $P=0.806$) or BMC ($\beta=0.009\pm0.056$, $Z=0.16$, $P=0.876$, GLMM with binomial errors controlling for year and group identity) with regard to their first solitary breeding attempt. Solitary breeders left the group before their communally-breeding nestmates gave birth (mean difference= -19.35 ± 4.45 days; $t_{20}=6.39$, $P<0.001$, paired t-test).

The interval between leaving the group and giving birth was longer for solitary breeders with relatives (12.9 ± 3.7 days, $n=25$) than for returners ($\beta=1.28\pm0.18$, $Z=6.99$, $P<0.001$, GLMM with poisson errors controlling for individual and group identities and year). Among solitary breeders ($n=25$), 56% gave birth within six (median 0) days of leaving the nest, while 28% did not appear to be gestating when they left the nest (26-37 day interval between leaving the nest and parturition). The interval between becoming solitary and giving birth increased with AP ($\beta=0.002\pm0.001$, $Z=2.2$, $P=0.025$; $n=25$, GLMM with poisson errors controlling for group identities and year) and the number of female nestmates ($\beta=0.146\pm0.002$, $Z=66.3$, $P<0.001$) and decreased with increasing BMC ($\beta=-0.065\pm0.02$, $Z=29.7$, $P<0.001$).

Was breeding synchrony associated with ARTs?

Communally-breeding females from the same group were more synchronized with each other in giving birth (5.8 ± 0.49 days apart, $n=61$ pairs of observations from 44 individuals) than

females from different groups were with each other (9.0 ± 0.57 days apart, $n=1938$ pairs from 132 individuals; $\beta=0.43 \pm 0.06$, $Z=7.68$, $P<0.001$). Communally-breeding nestmates were also more synchronized with each other than with returners from their own group (7.1 ± 0.56 days apart, $n=63$ pairs from 54 individuals; $\beta=0.19 \pm 0.07$, $Z=2.70$, $P=0.018$), but synchrony within communal breeders did not differ from synchrony between communal and solitary breeders from the same group (5.1 ± 0.70 days apart, $n=12$ pairs from 16 individuals; $\beta=0.13 \pm 0.13$, $Z=1.06$, $P=0.622$). Returners were no more likely to give birth before communally-breeding nestmates ($n=31$ pairs from 33 individuals) than after them ($n=31$ pairs from 37 individuals; $P=1.000$, exact binomial test; 1 pair of observations in which a communal breeder and a returner gave birth on the same day excluded), nor were solitary breeders more likely to give birth before communally-breeding nestmates ($n=5$ pairs from 8 individuals) than after them ($n=7$ pairs from 10 individuals; $P=0.774$).

Did the distribution of reproductive phenotypes change over the breeding season?

Communal breeders gave birth earlier in the season than females of any other category (Tukey contrasts based on LMM: $P \leq 0.004$; Fig. 3); solitary females with and without relatives and returners did not differ in the timing of their parturitions ($P \geq 0.297$; Fig. 3), controlling for T_a ($\beta=2.44 \pm 0.34$, $t=7.28$, $P<0.001$) and BMC ($\beta=0.66 \pm 0.18$, $t=3.60$, $P<0.001$), which were positively related to parturition date. Age did not influence parturition date ($\beta=-0.01 \pm 0.01$, $t=0.95$, $P=0.342$).

Solitary breeding as a consequence of extrinsic factors

Of the 45 females that bred solitarily, 57.8% had surviving female relatives in the population. The rest were constrained to breed solitarily because their female relatives died, and they did not join another group with unrelated females. Females that became solitary because their relatives died did not differ in BMC from communal breeders ($\beta=2.48\pm1.59$, $Z=1.56$, $P=0.242$; LLM with Dunnett contrasts; Fig. 2) or returners ($\beta=1.28\pm1.52$, $Z=0.84$, $P=0.680$). However, females that were group-living at conception and became solitary while their relatives were living weighed more than females whose relatives died ($\beta=4.81\pm2.01$, $Z=2.39$, $P=0.040$; Fig. 2). BMC did not differ before and after females' relatives died (before relatives died: 48.22 ± 3.50 g, $n=4$ records from 4 females, after: 48.50 ± 1.37 g, $n=17$ observations from 25 females; $\beta=-0.28\pm3.71$, $t=0.07$, $P=0.941$), controlling for AP ($\beta=0.03\pm0.01$, $t=2.25$, $P=0.033$). Solitary females without relatives did not differ in AP (299.5 ± 21.87 days) from communal breeders (297.2 ± 16.24 days; $\beta=2.32\pm21.79$, $Z=0.11$, $P=0.999$; LMM with Dunnett contrasts) or returners (298.4 ± 15.86 days; $\beta=1.14\pm20.93$, $Z=0.06$, $P=0.999$). There was a tendency for solitary females with living relatives to be younger (245.4 ± 20.71 days) than those whose relatives had died ($\beta=54.15\pm24.06$, $Z=2.25$, $P=0.056$).

Discussion

We tested whether the theoretical framework developed to explain strategies governing male ARTs also applies to females. Among female striped mice, three ARTs occurred simultaneously in the population: most females bred communally in a nest shared with relatives (communal breeders) or left the group temporarily to give birth (returners). A smaller proportion became solitary and did not return to the group after producing young,

even though relatives were still living (solitary breeders with relatives). Females switched between ARTs, which can occur under single but not alternative strategies, and so we tested whether this represented a conditional or mixed single strategy. Studies of conditional strategies in free-living individuals are often unable to measure potential cues (e.g. body mass) before individuals switch tactic, and are thus often confounded by environmental effects that occur after the switch. We addressed this by investigating body mass records collected before females became solitary. Females that went on to breed solitarily were heavier than communal breeders and returners, which suggests that body mass influences tactic choice. We could differentiate between two kinds of solitary breeder: those that became solitary while their relatives were alive and those that were forced by stochastic external factors (mortality of relatives) to rear young alone. We did not find an association between female reproductive phenotype and either parturition trapping interval and radio-tracking effort, which suggests that variation in survey effort did not bias our results towards a particular phenotype. Our results show that both phenotypic plasticity and extrinsic factors can produce intra-specific variation in social organization, and that evolutionary theory developed for ARTs in males also applies in females.

(i) Do ARTs arise from alternative strategies or a single strategy in female striped mice?

The majority of female striped mice that bred more than once switched reproductive tactics. The ability to switch ARTs has been described in females of several species of birds, fish and insects (Warner 1985; Åhlund & Andersson 2001; Zink 2003). This behaviour is consistent with a single strategy, where different tactics arise from one decision-rule (Schradin & Lindholm 2011). It is worth noting, however, that several females that bred more than once did not switch tactics. Instead they showed a single phenotype of solitary breeder, communal breeder or returner. Those females could be following i) alternative strategies with fixed

tactics or ii) a single strategy in the absence of (or without responding to) cues that elicit switching between tactics. Strategic models show that alternative and plastic strategies can coexist within a single population and be evolutionarily stable under a range of conditions (Lively 1986; Plaistow et al. 2004). This idea has received further theoretical support from a quantitative genetics perspective (Hazel, Smock & Lively 2004). Indeed, empirical work has described coexistence of conditional and unconditional strategies in barnacles (Lively et al. 2000), mites (Buzatto, Simmons & Tomkins 2012) and sailfin mollies (Fraser et al. 2014). In our study, many females that switched tactics had previously maintained one tactic for multiple breeding attempts before the switch. It therefore seems likely that at least some of the females that did not switch tactic were capable of doing so. In striped mice, high population density can constrain females to remain group-living (the best tactic under these conditions; Schradin et al 2010), while experimentally easing these constraints by decreasing local population density induces a switch to solitary-living (Schoepf & Schradin 2012a). The decision not to switch tactics can therefore represent an adaptive response to stable environmental conditions. While we cannot exclude the possibility that females that maintained the same tactic throughout the breeding season were using alternative strategies, we present evidence for the existence of a plastic strategy that is used by most females in the population.

A female's reproductive tactic was a predictor of her subsequent tactic, with individuals often following the same tactic for more than one consecutive breeding attempt. Females that switched tactics generally proceeded from communal breeder to returner to solitary. The relative distribution of ARTs changed over the breeding season, with communal breeding occurring earlier in the season than the other ARTs. Tactic switches between communal breeders and returners were often reversible. Solitary breeders, by definition, do not re-join

their former group, but can make the transition to communal breeder (or returner) by forming plural breeding groups with adult daughters. One female established a new group after her relatives died, and she and her daughters bred communally the following year. Females whose nestmates died did not join other groups, indicating the importance of genetic kinship in the formation of breeding groups. Although non-relatives can form transient overnight huddling groups in winter (Schradin, Schubert & Pillay 2006), aggression towards non-kin during the breeding season (Schradin 2004) probably constrains the direction of tactic switching.

(ii) Do ARTs represent a mixed or a conditional strategy?

Mixed and conditional strategies are two types of single strategy (Schradin & Lindholm 2011). When individuals follow a conditional strategy, ARTs can be determined by differences in traits that reflect competitive ability (Gross 1996). No such association is predicted under a mixed strategy, which assumes that tactics are stochastically assigned (Dominey 1984). We found that solitary breeders with relatives were heavier than communal breeders and returners before leaving the group, consistent with a conditional strategy (Fig. 4). Body mass or size is an important cue governing the switchpoint between ARTs in males (e.g. Tomkins & Brown 2004; Schradin et al. 2009b) and females (Warner 1985) of various taxa. This probably reflects its reliability as an indicator of competitive ability (Wada et al. 2005) and/or energy reserves (Nunes et al. 1999) in species with alternative life histories. Male and female Belding's ground squirrel (*Spermophilus beldingi*), for example, do not disperse until they reach a threshold body mass, and dispersing males have more fat reserves than males of the same age that delay dispersal (Nunes et al. 1999). Thermoregulation is more energetically expensive in solitary than group-living striped mice (Scantlebury et al. 2006), and solitary breeders must also meet the energetic requirements of nursing pups and

defending a territory alone. We therefore propose that female striped mice remain group-living until they have amassed enough body reserves to support the energetic demands of solitary breeding. Together these results show that body mass is a key trait underlying the evolution of conditional strategies in many species.

Leaving the group temporarily to give birth may allow females to avoid reproductive competition without foregoing the long-term benefits of group-living. Female lions (*Panthera leo*) become less gregarious during the first weeks postpartum and hide cubs from pridemates (Packer, Pusey & Eberly 2001). Breeding synchrony is thought to have evolved to reduce the risk of infanticide by co-breeding females (Lambin 1993; Poikonen *et al.* 2008), which stop being infanticidal after their own offspring are born (e.g. McCarthy & Saal 1985). In addition, asynchronous births are associated with higher pup mortality for later-born litters in some cooperatively breeding mammals because younger pups are outcompeted by older ones or suffer physical trauma from being crushed by them (Mennella *et al.* 1990; Hodge, Bell & Cant 2011). Indeed, we found that the degree of within-group breeding synchrony was lower for returners than communal breeders. This suggests that the returner tactic might have evolved as a counter-measure against infanticide and/or offspring competition with older litters. Interestingly, females that left the group without returning did not differ in synchrony from communal breeders, which suggests that synchrony did not underlie their decision to breed solitarily.

(iii) Solitary breeding as a consequence of extrinsic factors

Group-living females can become solitary of their own volition or because of external constraints. Among the females that bred solitarily in our study, 57.8% had surviving female relatives in the population and the rest became solitary because their relatives had died.

Importantly, the latter group weighed less than solitary breeders with living relatives, but did not differ from group-living females in body mass. This suggests that solitary breeders without relatives would have usually remained group-living if their relatives had survived. The trend towards females with no relatives being older than solitary females with relatives may be a consequence of the former having outlived their relatives. In summary, extrinsic factors can produce a solitary-breeding phenotype that differs in individual-level traits from females that become solitary through choice.

Potential fitness outcomes

Alternative phenotypes can persist within a population when relative fitness rankings reverse across different spatial or temporal units (Moran 1992). Relative fitness varies between years in male striped mice: in years with high population density dominant breeding males sired more pups than roamers and philopatric males, whereas all males were roamers in years with low population density (Schradin & Lindholm 2011). It is not yet known whether fitness differs between ARTs in female striped mice, and whether relative fitness rankings vary under different ecological conditions (e.g. population density). In our study, communal breeders gave birth ~11 days earlier than returners and ~16 days before solitary breeders. The abundance of food plants at our study site decreased linearly over the breeding season (D.L. Hill, Pillay, N. & Schradin, C., unpublished data). This raises the possibility that communal breeders' offspring could experience greater food availability. This may be traded-off with the greater risk of infanticide in communally-breeding groups (Schradin et al. 2010). Comparisons of fitness correlates between solitary and communally-breeding female rodents have yielded mixed results (e.g. Boyce & Boyce 1988, Manning et al. 1995). Whether free-living offspring born in communal and solitary nests differ in growth trajectories, condition or survival remains to be tested in female striped mice.

Conclusions and implications

Male ARTs usually evolve where investment by dominant resource-holding ('bourgeois') males can be exploited by other males (Taborsky, Oliveira & Brockmann 2008). However, owing to anisogamy, and gestation in viviparous species, all breeding females must make a substantial investment in reproduction, resulting in smaller asymmetries in effort and fitness between females compared to males (Taborsky, Oliveira & Brockmann 2008). Consequently, ARTs are usually more subtle in females than in males and more likely to occur after fertilisation. Female striped mice show three ARTs whose expression is controlled by a single strategy (Fig. 4) in at least the majority of the population. This strategy may enable females to avoid reproductive competition when certain individual-level and environmental conditions are met. Male and female ARTs share many similarities in striped mice, but also differ in certain respects. Males, like females, follow three ARTs that differ in body mass; they can breed solitarily (as roamers) or in a group (as dominant breeders or philopatrics; Schradin et al. 2009b). Philopatric males differ in age from dominant breeders and roamers (Schradin et al. 2009b), but age did not influence female ARTs in our study. At a proximate level, males following alternative tactics differ in corticosterone and testosterone levels (Schradin et al. 2009b), whereas female ARTs differ in corticosterone and oestrogen levels but not in testosterone (Hill, Pillay & Schradin 2015). These differences and the occurrence of the returner tactic in females suggest that ARTs in female striped mice are unlikely to simply reflect a correlated response to selection for ARTs in males.

An important feature of populations in which reproductive and social tactics occur in both sexes is the potential for the entire social system to change facultatively as a result of decisions made at the individual level (Schradin et al 2012). Social flexibility has been

628 described in various taxa, including dunnocks (*Prunella modularis*), burying beetles
629 (*Nicrophorus vespilloides*) and humans (*Homo sapiens*, reviewed in Schradin et al. 2012). It
630 is particularly prevalent in species where individuals need to respond quickly to
631 unpredictable, fluctuating environmental conditions that might differ substantially from those
632 experienced by previous and subsequent generations (Schradin et al. 2012). Improving our
633 understanding of the evolution of phenotypic plasticity and how it facilitates resilience to
634 environmental change is an important and timely goal.

Acknowledgements

We wish to thank staff at Goegap Nature Reserve for practical support and the Northern Cape Nature Conservation Service for research permits. We are grateful to South Africa's National Research Foundation (Freestanding Fellowship, grant number 75057 to DLH), the University of the Witwatersrand (University Research Committee Fellowship to DLH), the Swiss National Science Foundation (31003A-135770/1 to CS), the Fonds zur Förderung des akademischen Nachwuchses des Zürcher Universitätsvereins (to CS) and the University of Zurich for funding. We thank Ed Yuen, Ivana Schoepf and numerous field assistants for help with data collection, and two anonymous reviewers for their constructive and insightful comments. The study was approved by the Animal Ethics Committee at the University of the Witwatersrand (2004/87/2A, 2005/82/4 and 2007/10/01).

648 **Data accessibility**

649

650 Data to be made available from the Dryad Digital Repository (Hill, Pillay & Schradin

651 unpublished).

652

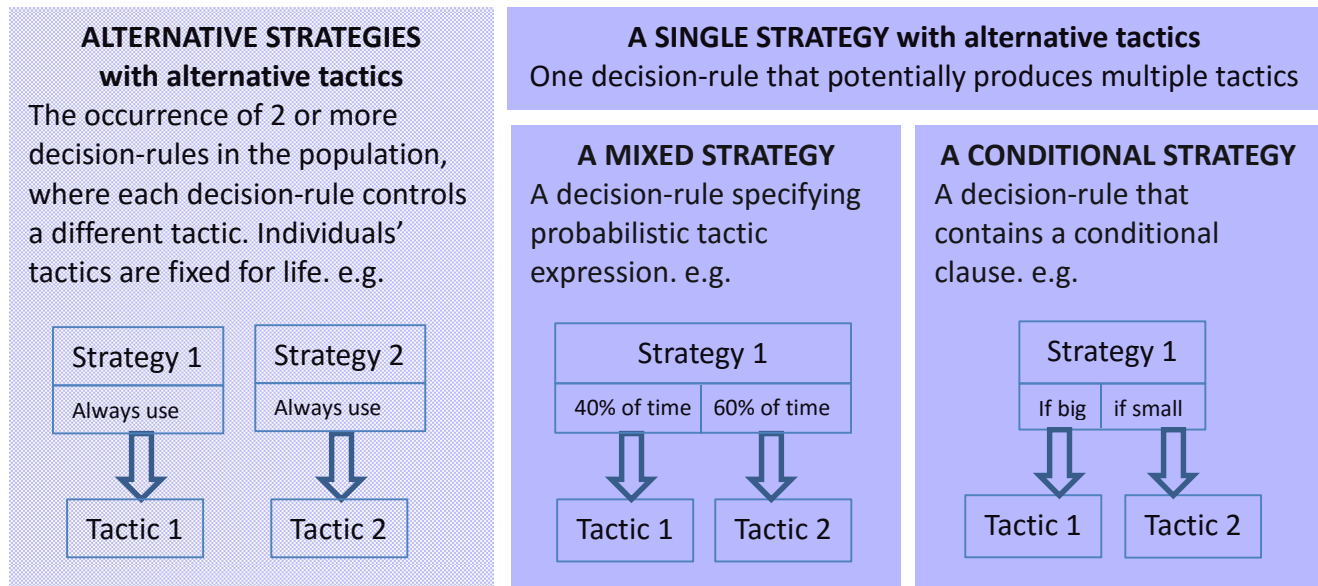


Fig. 1. Genetically-based decision-rules called strategies govern alternative reproductive tactics in members of the same sex and population. In species with *alternative strategies*, each strategy controls a different tactic with canalized expression (i.e. phenotypes are robust to environmental or genetic perturbations). In species with a *single strategy*, individuals use one decision-rule that controls the expression of multiple phenotypes (Schradin et al. 2012). Single strategies can be divided into mixed or conditional strategies. Mixed strategies specify that individuals switch tactics according to a particular probability distribution or are assigned permanently-adopted tactics probabilistically (Dominey 1984). Conditional strategies occur when each individual selects the tactic that generates the highest fitness returns for its prevailing circumstances (Gross 1996). The scenarios represented above are not necessarily mutually exclusive within a population (e.g. Plaistow et al. 2004)

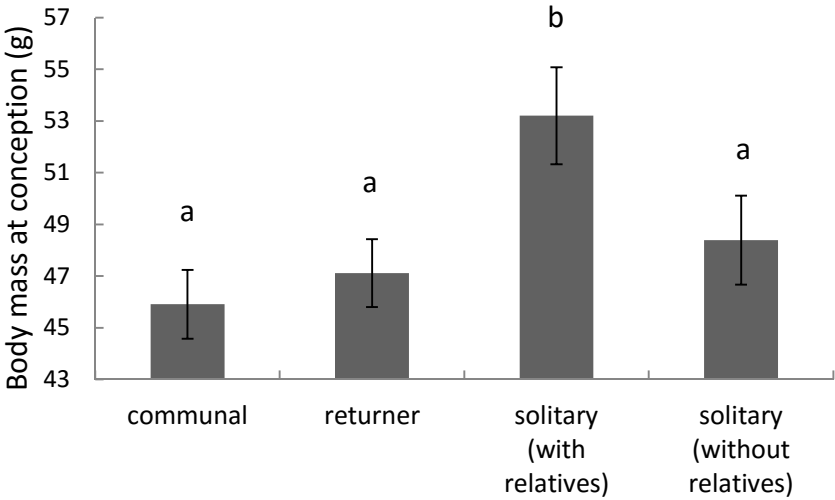


Fig. 2. Mean body mass at conception ± 1 SE in communal breeders ($n=87$ parturitions by 64 individuals), returners ($n=90$ parturitions from 66 females) and solitary breeders with living relatives ($n=18$ parturitions by 18 females that were still group-living when body mass was measured) and without living relatives ($n=29$ parturitions by 20 females). Different letters above bars represent significant differences adjusted for False Discovery Rate. Note that the y-axis is truncated

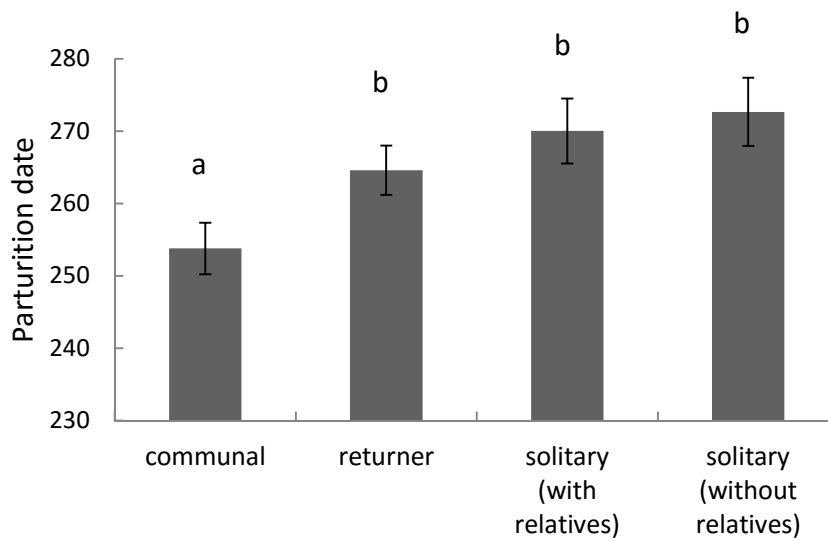


Fig. 3. Mean parturition date ± 1 SE (1 Jan of any year=day 1) in communal breeders ($n=87$ parturitions by 64 individuals), returners ($n=90$ parturitions by 66 individuals) and solitary breeders with living relatives ($n=37$ parturitions by 26 individuals) and without relatives ($n=29$ parturitions by 20 individuals). Different letters above bars represent significant differences adjusted for multiple testing

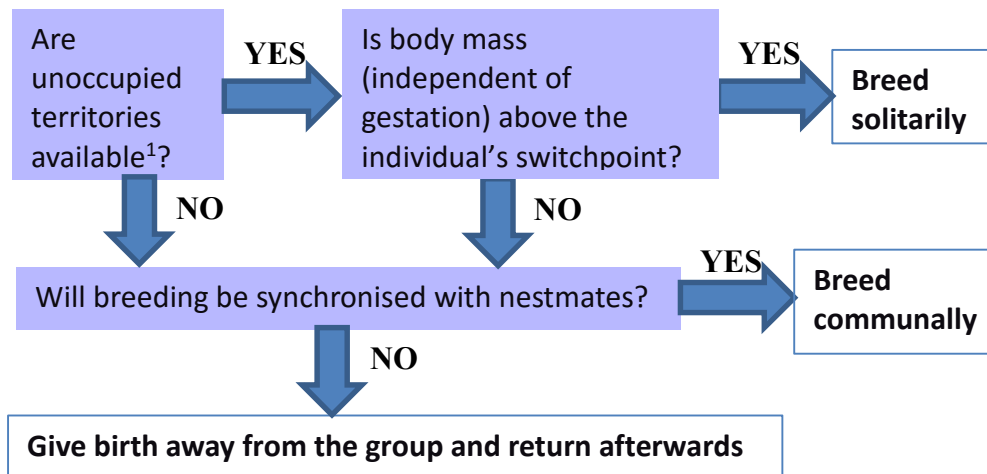


Fig. 4. The strategy (evolved set of decision-rules) predicted to govern the expression of the three alternative reproductive tactics used by female striped mice with living relatives. This ties together results from the present study and ¹Schradin, König & Pillay (2010). Females switched tactic upon reaching thresholds of body mass or breeding asynchrony with nestmates. Those that became solitary breeders were heavier when they conceived than communal breeders and returners, which did not differ in body mass. Females that were less closely synchronized with nestmates were more likely to use a returner tactic than to give birth communally. Selection is thought to act upon heritable genetic variation for the position of the switchpoint, so different individuals might change tactics at different values of the underlying traits (Tomkins & Hazel 2007). Solitary-breeding phenotypes can arise either from this strategy or as a consequence of extrinsic stochastic processes (mortality of all adult female relatives)

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Supporting Information

The following Supporting Information is available for this article online:

Appendix S1. Methods for multiple imputation of missing body mass and age values

Appendix S2. Specifications for multinomial mixed effects model

Figure S1. Correspondence between 97 consecutive pairs of alternative reproductive tactics (ARTs) represented by χ^2 distances between points in female striped mice